SURFACE ILLUMINATION AND BARNACLE ATTACHMENT

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During the past twenty years the effect of light conditions upon the attachment of barnacles has received a considerable amount of attention. The investigations of Visscher (1928) have shown that barnacles attach more readily to dark-colored than to green, white, or other light-colored surfaces. This has since been confirmed by Edmondson and Ingram (1939). Pomerat and Reiner (1942) report greater numbers of attachments of *Balanus eburneus* to the underside of horizontal black plates than to opal plates during daylight. Fewer numbers attached to the upper surface of black plates than to the lower surface. The distinction between black and opal was not apparent during darkness. These authors also found that attachment to opal and transparent collectors were similar on both upper and lower surfaces. Confirmatory results were obtained by Pomerat and Gregg (1942) and by Edmondson (1944).

The observations of McDougall (1943) substantiate those previously mentioned. Nevertheless, although during the day time the rate of attachment was greater in shade than in sunlight, it was considerably lower at night upon any surface. This might suggest that the stimulus to attachment was not a uniform condition of relative shade but rather the contrast in lighting conditions present only during daylight. Nevertheless, attempts by Gregg (1945) to demonstrate a stimulus to attachment in the contrasting effect of adjacent light and dark surfaces were inconclusive.

Since 1942 investigators at Miami have repeatedly observed, in the case of *Balanus amphitrite niveus* Darwin and *B. improvisus* Darwin, not only a greater rate of attachment to darker surfaces during daylight, but also a diminished rate of attachment to all surfaces during the hours of darkness. Furthermore, attachments in darkness were found to be even less than attachments to light colored surfaces during daytime.

In the absence of the last mentioned observation, the lesser attachment to lighter colors in daylight and the equal attachments to all surfaces during darkness might be explained in terms of a negative phototropotaxis, using the terminology of Fraenkel and Gunn (1940). This would bring about movement away from light surfaces in daylight and would account for failure to distinguish any particular surface during night time. It would not, however, explain the greater number of attachments to *light* surfaces in daylight than in darkness. The theory of negative phototropotactic behavior is apparently supported by the laboratory observations of Runnstrom (1925), Visscher (1928b), Visscher and Luce (1928), Hertz (1933) and Neu (1933), who show that while the nauplius larvae swim towards the lighted side of a vessel, cyprid larvae swim away and attach on the opposite side, their activity being greater in green light than in other portions of the spectrum.

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Observations communicated by Gregg (in literis) show that under conditions of weak artificial illumination at night, attachments to white plates are greater than to black, thus reversing the daytime condition. This and the previously mentioned anomalies, which are not readily explained by simple negative phototropotaxis, prompted the experiments here described, whereby the numerical distribution of cyprids between adjacent black and white surfaces of various sizes in daylight was investigated as a preliminary to further observations under carefully controlled artificial illumination.

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Methods

The apparatus consisted of a series of similar glass plates eight inches square, painted checkerboard fashion with alternating black and white squares of equal sizes. The size of the squares varied from the extreme case in which the plate was painted entirely black or entirely white, to the other extreme, where the plate was painted with 64 one-inch squares. The plates were suspended in a wooden frame just below the surface of the sea water at the Miami Beach Boat Slips in such a way as to lie in a vertical plane parallel to the direction of tidal currents.

The experiments were repeated at two different sites, one inside a covered dock and the other in the open at the side of a dock. In the latter case, one side of the rack holding the panels was facing the open sea and the other was facing the darker underside of the dock. The arrangement of plates with respect to each other was a random one determined by removing numbered cards from a hat. By painting the reverse side of each plate with a different system of squares a different sequence of plates was provided on the two sides of the rack, thus providing two sets of observations.

The rack of plates was suspended in the covered dock from 9 A.M. to 5 P.M. on a calm, sunny day. On the following day, under the same weather conditions, it was exposed for a similar period in the open dock so that a total of four sets of observations was taken. Counts of the attached cyprids were made immediately upon removing from the water.

Results

Individual observations are recorded in Table I and the average of the four exposures is recorded at the end of the table. In the average of four exposures, the average density of attachments upon the entire surface of each panel, including both black and white areas, varied from the panel of one-inch squares with 5.7 per square inch to the panel of four-inch squares with 4.7. The attachments on an equal area of the panel consisting of an eight-inch black square were 4.6, Figure 1. The checkered panels as a whole, therefore, acquired attachments somewhat greater in density than the single black panel, with a decrease in average density as the size of squares increased. On the plain white panel the average attachment density was 1.4 per square inch, or considerably less than in the case of the checkered or black panels.

Table I shows that with decreasing numbers and increasing size of squares the numbers of attachments to white surfaces decreased. Thus, on the plate with one

TABLE I

Variation in density of barnacle attachments upon black and white squares of checkerboard collectors in relation to size of squares

Expressed in attachments per square inch

Experiment	Surface	Size of squares			
		8 inch entirely black or white	4 inch	2 inch	1 inch
Covered dock	Black	4.4	5.8	4.1	4.6
Side A	White	0.7	2.2	4.4	4.6
2/16/44	Average entire panel	2.5	4.0	4.2	4.6
	Ratio black/white	6.6	2.6	0.9	1.0
Covered dock	Black	3.6	6.1	6.0	5.5
Side B	White	1.2	2.5	4.8	4.4
2/16/44	Entire panel	2.4	4.3	5.4	4.9
	Ratio black/white	3.3	2.5	1.3	1.2
Open dock	Black	2.9	5.2	3.5	4.6
Side A	White	1.1	2.2	4.4	6.0
2/17/44	Average entire panel	2.0	3.7	3.9	5.3
	Ratio black/white	2.6	2.5	0.9	0.8
Open dock	Black	7.3	8.8	6.4	6.8
Side B	White	2.6	5.0	6.0	9.3
2/17/44	Average entire panel	4.9	6.9	6.2	8.0
	Ratio black/white	2.6	1.7	1.6	0.8
Average of 4	Black	4.6	6.4	5.0	5.4
exposures	White	1.4	3.0	4.9	6.1
	Average entire panel	3.0	4.7	4.9	5.7
	Ratio black/white	3.3	2.2	1.0	0.9

inch squares, the average number of attachments to white areas was 6.1 per square inch. The density of attachment to an equivalent area on the plain white plate, consisting of one eight-inch square only, was 1.4. This is less than one quarter of the attachment to one-inch squares. On the plates with two- and four-inch squares the attachments were intermediate in number.

Attachments to black squares showed less variation. The attachment was greatest on the 4-square panel with four-inch squares, where the average density was 6.5, and least on the plain black eight-inch panel, with an average of 4.6 per square inch, or about three-quarters of the attachment to four-inch squares. Thus not only was variation considerably less than in the case of white squares, but it did not bear a continuous relation to the size of squares, and may not be significant.

It follows from the variation in attachments to white squares that the ratio of attachments upon black areas to attachments upon white areas decreased with diminishing size of squares. It was greater than 3 on the eight-inch squares whereas on the one- and two-inch squares black and white attachments were almost equal.

In order to demonstrate the absence of simple tropotactic response to surface illumination, the ratio of attachments to black over attachments to white is plotted

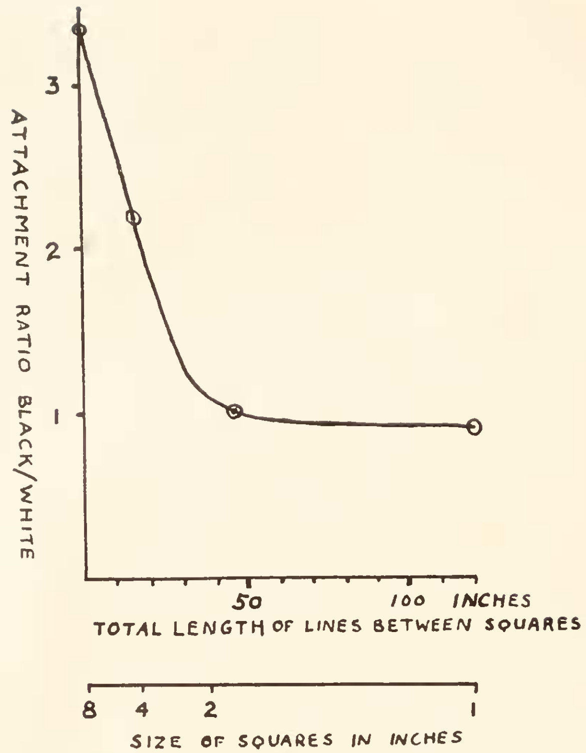

FIGURE 1. Ratio of attachments to black and to white squares in relation to size of squares and to length of black-white boundary lines.

in Figure 1 against the linear extent of the lines separating black and white squares on each plate. From this figure it is apparent that the ratio diminishes as the black/white separation length increases, reaching unity at a point corresponding to a square of side about 2 inches.

An examination of the data for the individual experiments shows a similar behavior in each case. The panels exposed in the covered dock did not differ significantly in numerical attachments, but showed a slightly lower attachment to large white squares, and consequently a slightly higher black/white ratio for the larger squares. It is doubtful whether the difference is sufficient to be of significance.

Discussion

It is apparent that the results do not uphold the simple conception that a cyprid swims actively towards dark surfaces only or swims away from white surfaces, or is capable of orientation so as to move towards a black surface in preference to a white surface. The results indicate rather that with increasing opportunity of exerting such a "choice" the cyprids show an increasing lack of ability to discriminate between black and white surfaces (Fig. 1). The apparent discrimination is limited to squares over 2 inches in size.

The attachments to black surfaces appear to be little affected by adjacent white surfaces except possibly in the case of four-inch squares. A greater density of attachments to black is associated with the presence of four-inch white squares rather than with black alone, or with black coupled to white squares smaller than four inches. The difference is rather small, however, and may not be significant.

The most striking result of the experiments is the very considerable decrease in attachment density on white squares as the size of squares increases. This is in harmony with the possibility that the cyprid is influenced not by directional light rays from the panel surface but by the general light flux or intensity of diffuse light at some distance from it. In this manner diffused light resulting from scattered reflections adjacent to larger white squares would be more intense and more effective than diffused light produced by reflection adjacent to the smaller white squares where the black surfaces would be sufficiently close to exert a "diluting" effect on the light flux. On the basis of this explanation the cyprids may be stimulated to attach when they enter into an area characterized by low intensity of diffuse light, or they may be inhibited from attaching to an increasing extent as the intensity of diffuse light increases. They would thus be subjected to the inhibiting effect as they approached large white squares, but smaller white squares as indicated above would be less effective because of the increasingly fine admixture of black surfaces which would provide a light flux in the immediate neighborhood approximating to that which a hypothetical gray surface would produce.

Greater attachment density to the small size checkerboards than to plain black surfaces may possibly indicate that there is an optimum intensity of diffuse light represented by that of the small square checkerboards equivalent to that produced by gray surfaces and that unrelieved black panels are less effective in providing attachments because the light intensity is below the optimum. The existence of an optimum light intensity would also explain the low attachment density characteristic of panels exposed during darkness which would be below the optimum. The anomalies reported by Gregg whereby, under conditions of weak artificial illumination at night, barnacles attach in greater numbers to white than to black panels may also be explained by the existence of an optimum intensity of light for attachment. White squares under weak artificial illumination might provide diffuse light of intensity nearer the optimum than black, whereas in daylight white would produce light above the optimum, black slightly below the optimum, and small checkerboards or gray would produce approximately the optimum. It is unfortunate that conditions did not permit an accurate determination of the illumination. It may be possible to remedy this in future experiments in which it is proposed to provide controlled artificial illumination during hours of darkness.

The experiments of Visscher and others (op. cit.) have demonstrated a simple negative phototropotaxis under laboratory conditions which is not borne out by the present investigations. The apparent contradiction, however, may be readily resolved when the natural conditions of submarine illumination are taken into consideration. As Whitney (1941) and Schallek (1942) have pointed out, light is usually polydirectional under sea water and only rarely is there a truly unidirectional beam. The sediment present under coastal and estuarine conditions where barnacles naturally occur serves to intensify the diffuse nature of the light. While working in diving helmets in 15 feet of water at the site of the present experiments it was found most difficult to orient with respect to the shaded and open part of the dock. The intensity of illumination appeared to be almost equal in every direction, yet after taking a few steps into the shade of the dock the intensity would suddenly decrease very considerably. Even at a point immediately below the edge of the dock little difference was experienced in the light intensity when facing towards or away from the covered area.

It is possible that other and more reasonable interpretations of the experiments presented here may exist, but it is believed that the results, at least, indicate the necessity of a renewed examination of the light reactions of barnacle cyprids during attachment, preferably by means of carefully controlled laboratory experiments in which both diffuse and unidirectional light are considered and in which the possibility of a low optimum intensity favoring attachment is borne in mind.

Summary

1. Experiments were designed for the purpose of investigating the various anomalies reported in the response of barnacle larvae to black and to white surfaces. The apparatus consisted of panels of similar size but checkered with black and white squares of sides varying from eight inches to one inch.

2. Average attachment density over the entire panel increased slightly with diminishing size of squares. Attachment density to white squares increased with diminishing size of squares. Attachments to black squares did not vary continuously with size of squares. The distribution ratio between black and white decreased from over 3 on eight-inch squares to unity on 2-inch squares.

3. As an explanation of the results and of previously reported anomalies it is suggested that cyprids are stimulated to attachment by a low optimum light intensity of light, and that diffuse light rather than unidirectional light is the principal factor involved.

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